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Non-native fish species expand tacitly but rapidly toward upstream oxbow lakes along the longitudinal gradient

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Abstract

The introduction of non-native fish species poses a threat to native assemblages in floodplain systems. Establishing oxbow lake-based conservation areas has been proposed as a practical approach to mitigate this threat. Previous studies have extensively discussed the effects of lateral connectivity between oxbow lakes and main channels on fish communities but overlooked the spatial longitudinal gradients of oxbow lakes on a broader spatial scale. Over the course of about ten years, the temporal changes in fish community diversity were estimated in 28 oxbow lakes along the Ishikari River in Hokkaido, Japan. The associations between these temporal variations and the locations of the lakes were then explored along a longitudinal spatial gradient. The results showed that upstream oxbow lakes underwent mild alterations to their species composition and maintained a high level of native uniqueness. In contrast, downstream oxbow lakes experienced intense species turnover and increased non-native fish diversity. Additionally, the dominance of non-native fish in downstream areas rapidly expanded upstream to a location 110 km from the source of the Ishikari River over the decade. It is emphasized that the lakes in the upper reaches were the only remaining refuges for native fish and should be prioritized in conservation efforts. Our study proposes the application of location and species contributions to regional community heterogeneity as indicators for highlighting native fish conservation areas.

Keywords

beta diversity, floodplain, LCBD, native conservation, SCBD

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Introduction

Freshwater ecosystems are among the most threatened ecosystems worldwide during the current Anthropocene (Grill et al. 2019; Su et al. 2021). One of the most urgent global challenges confronting humanity is the unparalleled alteration of these aquatic environments (Su et al. 2021). Native fishes are particularly vulnerable to non-native species invasions, which are among the most pervasive drivers of biodiversity losses in most freshwater ecosystems (Dudgeon et al. 2006; Leprieur et al. 2008). In recent decades, non-native fish species have been intentionally relocated across watersheds, countries, and continents for economic, biological control, recreational, and ornamental purposes (Gozlan et al. 2010; Xiong et al. 2015). Non-native fish introductions also occur due to unintentional actions like aquaculture escapes, canal or waterway connections, and ballast water discharges from vessels (Hulme et al. 2008; Musil et al. 2010). The combination of intentional and unintentional introductions of non-native species has led to significant declines in local native fish species in various regions around the world (Moi et al. 2021; Sleezer et al. 2021; Angulo-Valencia et al. 2022; Kang et al. 2022; Zhang et al. 2022). Considering their unique provision of optional value during their evolutionary histories, the need to mitigate diversity loss and enforce conservation intervention for native fish species has been widely acknowledged (Fensham et al. 2011; Xing et al. 2016).

The concept of native fish conservation areas (NFCAs) has been developed with the aim of protecting endemism from exotic species invasion (Williams et al. 2011). In order to effectively implement NFCAs, there is a need for comprehensive information about the geographical location and extent of potential protected regions. One major challenge in demarcating NFCAs is the expansive spatial region encompassed by interconnecting drainage systems. Focusing only on partial areas within a drainage region without considering the integrity of the drainage systems (Abell et al. 2007) can lead to inconsistent protection efforts within subregions and can hinder the conservation of the entire system (Williams et al. 1989). Furthermore, the spatiotemporally dynamic utilization of heterogeneous aquatic habitats by aquatic organisms, particularly fish species that rely on movement across diverse habitats to complete their life cycles (Roni 2019), necessitates the inclusion of essential habitats for native species to manifest all crucial life cycle stages, as well as critical areas for migration, spawning, and rearing within the basin (Olden et al. 2010; Williams et al. 2011). The protection of native fish cannot be ensured through the sole consideration of limited, specific locations. Therefore, it is recommended that when selecting NFCAs, a comprehensive assessment of all accessible water bodies in the watershed be conducted, followed by identifying waters with high conservation values.

NFCAs are often established covering shallow lakes or floodplain oxbow lakes along the river mainstem because of the stable hydrological environments. For instance, NFCAs have been implemented in such lakes along the mainstream of Amazonian tropical streams to warrant native fish preservation and protection (Barocas et al. 2021). These lakes provide ideal habitat and sustenance, facilitating the interconnectivity of fish species interactions (Dai et al. 2020). Abundant studies have ascertained the nomination of

floodplain lakes as prospective candidates for NFCAs by assessing the lateral connectivity between lakes and the main channels, which might elevate groundwater levels, offer additional habitats, and maintain connectivity to source populations (Miranda 2005; Pander et al. 2018; Wang et al. 2020). Nevertheless, in addition to lateral connectivity, the longitudinal gradient of the physiochemical properties of the aquatic habitats from upstream to downstream (Vannote et al. 1980; Doretto et al. 2020) prompts us to anticipate diverse roles and functions of floodplain lakes along the longitudinal river gradient, which are frequently overlooked. Hence, we suggest that it is of great importance to explore fish metacommunity variations in floodplain lakes along longitudinal gradients to highlight the prioritization of oxbow lakes for NFCAs in river-floodplains.

Longitudinal upstream-downstream gradients in river-floodplain ecosystems are characterized by continuous environmental gradients in climate, hydrological regime, and sediments (Suvarnaraksha et al. 2012; Oberdorff et al. 2019). However, river landscape gradients have been modified intensively in the Anthropocene, with pristine natural environments in the upper reaches and disturbed urbanized areas in the lower reaches (Wan and Zhong 2014; Wang et al. 2017; Xiao et al. 2021). Such longitudinal variations in hydrological features and landscapes have also been frequently observed in shallow lakes and oxbow lakes along the main river (Pongsivapai et al. 2021). The downstream urban area in floodplain systems usually provides habitats favored by introduced non-native species and substitution for native fish niches (Olden et al. 2006; Pingram et al. 2021). Native species that are sensitive to environmental conditions may prefer lakes located in upstream areas with minor anthropogenic disturbance (Shochat et al. 2010; Goetz et al. 2015; Ishiyama et al. 2020; Zhang et al. 2022). We believe that such spatial longitudinal variations must also be considered when establishing oxbow lake-based NFCAs for more efficient and targeted native conservation in these lakes.

The Ishikari River basin (the second largest in Japan) is characterized by a substantial presence of oxbow lakes, which exhibit a significant longitudinal distribution pattern along the river. The Ishikari River basin underwent considerable urban transformation throughout the last century, predominantly within its downstream regions, which have now become subject to the highest population density in Hokkaido. Despite the intense anthropogenic activities that have substantially decelerated in the 21st century, it is recognized that preceding alterations to the watershed environments, attributable to industrialization, contamination, and other factors, have already exerted deleterious impacts on the river-floodplain ecosystems. In the early 2000s, Hayashida et al. (2010) researched the fish species community composition in the oxbow lakes and evidenced the presence of non-native fish invasion in the Ishikari River basin. A subsequent study by Fujii et al. (2019) about a decade later further reported the fish species composition of these oxbow lakes based on both traditional and molecular approaches. However, neither study considered the potential link between the fish community of individual lakes and their longitudinal spatial distribution along the river. This study, building upon the findings of two prior research studies, seeks to analyze the interactions between native and non-native fish populations in oxbow lakes during the period from 2003 to 2016, a period with minimal external environmental changes. Additionally, the study aims

to discern whether any observed changes in these interactions present a longitudinal pattern, shifting from upstream to downstream, considering the spatial distribution of these oxbow lakes along the Ishikari River. This analysis will further inform the identification of critical locations for native fish conservation areas (NFCAs). Our hypothesis posits that (1) Temporally, native fish would be sporadically distributed in specific lakes and result in a decline in native richness but an increase in regional dissimilarity. On the other hand, the introduction and expansion of non-native fish will result in an increase in non-native richness and temporal similarity; (2) Spatially, we hypothesize that both native and non-native fish species will exhibit longitudinal patterns in metacommunity changes. This is based on the fact that non-native species, with their high environmental adaptability, are likely to be more prominent in downstream areas, while native fish prefer upstream lakes that offer diverse conditions resembling their natural habitat.

Methods

Study areas and fish datasets

The Ishikari River in Japan drains 14,330 km^2, flowing from its source on Mt. Ishikari to the Sea of Japan (Fig. 1). Oxbow lakes formed in great numbers longitudinally along the middle-lower Ishikari River. We selected a total of 28 oxbow lakes along the Ishikari River as our sampling sites (see Table 1). These lakes are situated 90 to 140 kilometers away from the river's source. These lakes are currently being maintained with similarly low to moderate lateral connectivity to the Ishikari mainstream because of the presence of flood dikes and sluice gates on outflow channels. Notably, during the studied period (2003–2016), negligible land use change occurred (Pongsivapai et al. 2021), and no extensive fish introductions were conducted in the Ishikari River basin. Based on detailed sampling methods described in depth in Hayashida et al. (2010) and Fujii et al. (2019), fish collections were conducted once at each lake in each of two periods: 2003/2004/2005 (the 2000s for abbreviation) and 2016 (the 2010s), respectively. Capture efforts were made to obtain the maximum number of fish individuals. We are cognizant of the fact that the personnel and instruments conducting fish collection in the two periods were not identical. To avoid biased results due to differences in sampling intensity and equipment, we extracted the fish incidence (presence/absence) rather than abundance for further statistical analysis. Despite the lack of abundance information, the use of incidence data ensured the comparability of fish diversity results between the two periods without generating contradictory outcomes when compared to abundance-based results (Dai et al. 2020; Xia et al. 2022). Fish datasets are also partially extracted from Hayashida et al. (2010) and Fujii et al. (2019). We then identified the native and non-native fish species, compiling the distributional matrix for native and non-native fish assemblages, respectively. Refer to the fish incidence data for the 2000s and 2010s in Suppl. materials 1 and 2, respectively. The geographical coordinates for the studied lakes can be found in Suppl. material 3.

Table 1. Distances of the 28 oxbow lakes from the Ishikari River Source (DRS). The number of native and non-native species, with their proportions indicated in parentheses are also enumerated. An increase in the fish richness in a particular lake from the 2000s to the 2010s is marked with a superscript [+]. Statistically significant average increases in regional fish richness are highlighted in bold ($p < 0.05$, determined using PERMANOVA tests with 9,999 permutations). In general, we highlighted an increase in the regional average fish richness, which was accompanied by a rise in the number of non-native fish species.

Oxbow lake	DRS (km)	2000s			2010s		
		Overall	Native	Non-native	Overall	Native	Non-native
Tanba	92.56	9	8 (88.9)	1 (11.1)	11 [+]	7 (63.6)	4 (36.4) [+]
Ikenomae	92.70	14	8 (57.1)	6 (42.9)	14	8 (57.1)	6 (42.9)
Takonokubi	92.93	11	7 (63.6)	4 (36.4)	12 [+]	7 (58.3)	5 (41.7) [+]
Shisun	94.82	11	4 (36.4)	7 (63.6)	14 [+]	7 (50.0) [+]	7 (50.0)
Fukuroji	95.87	10	5 (50.0)	5 (50.0)	15 [+]	7 (46.7)	8 (53.3) [+]
Shimotoppu	97.04	12	6 (50.0)	6 (50.0)	17 [+]	9 (52.9) [+]	8 (47.1)
Mizuho	99.38	14	9 (64.3)	5 (35.7)	10	6 (60.0)	4 (40.0) [+]
Pira	99.95	12	7 (58.3)	5 (41.7)	11	6 (54.5)	5 (45.5) [+]
Toi	101.26	10	5 (50.0)	5 (50.0)	15 [+]	7 (46.7)	8 (53.3) [+]
Urausu	102.82	8	5 (62.5)	3 (37.5)	13 [+]	6 (46.2)	7 (53.8) [+]
Shin	104.91	15	9 (60.0)	6 (40.0)	18 [+]	10 (55.6)	8 (44.4) [+]
Higashi	106.35	13	7 (53.8)	6 (46.2)	15 [+]	8 (53.3)	7 (46.7) [+]
Sakura	106.71	7	6 (85.7)	1 (14.3)	11 [+]	6 (54.5)	5 (45.5) [+]
Nishi	107.10	12	6 (50.0)	6 (50.0)	13 [+]	5 (38.5)	8 (61.5) [+]
Hishi	107.51	8	4 (50.0)	4 (50.0)	13 [+]	6 (46.2)	7 (53.8) [+]
Ito	108.61	10	5 (50.0)	5 (50.0)	13 [+]	6 (46.2)	7 (53.8) [+]
Miyajima	114.22	12	6 (50.0)	6 (50.0)	8	4 (50.0)	4 (50.0)
Sankaku	114.49	4	4 (100)	0 (0.0)	4	3 (75.5)	1 (25.0) [+]
Omagari	115.66	12	5 (41.7)	7 (58.3)	12	6 (50.0) [+]	6 (50.0)
Kagami	119.10	6	5 (83.3)	1 (16.7)	3	3 (100)	0 (0)
Bibai	120.21	11	6 (54.5)	5 (45.5)	11	4 (36.4)	7 (63.6) [+]
Tsukio	121.94	13	8 (61.5)	5 (38.5)	8	6 (75.5)	2 (25.5)
Onuma	122.23	7	4 (57.1)	3 (42.9)	8 [+]	6 (75.0)	2 (25.0)
Tsukiko	122.71	9	6 (66.7)	3 (33.3)	14 [+]	9 (64.3)	5 (35.7) [+]
Tomoenojyo	127.77	10	5 (50.0)	5 (50.0)	10	4 (40.0)	6 (60.0) [+]
Echigo	132.68	8	6 (75.0)	2 (25.0)	8	6 (75.0)	2 (25.0)
Shinotsugawa	136.70	9	5 (55.6)	4 (44.4)	9	3 (33.3)	6 (66.7) [+]
Kyutoyohira	138.06	10	4 (40.0)	6 (60.0)	7	2 (28.6)	5 (71.4) [+]
Average		10.3	5.9 (59.5)	4.4 (40.5)	**11.3** [+]	6.0 (54.7)	**5.4 (45.3)** [+]

Dissimilarity measurements

Regional multi-site fish dissimilarity of two periods

Multi-site community dissimilarity assessment implies regional species co-occurrence patterns among multiple lakes. Hence, it is usually considered superior to the traditional comparisons between independent community pairs (Baselga 2013). Also, given that this study was spatially limited to a local watershed scale and that the datasets were arranged based on fish incidence, the Sørensen index is believed

Figure 1. Location of the 28 studied oxbow lakes along the Ishikari River.

to be appropriate for this study to generate robust and informative results (Jost et al. 2011). Consequently, we calculated multiple-site Sørensen dissimilarity indices to evaluate regional dissimilarities ($\beta_{SØR}$) of fish assemblages among all 28 oxbow lakes for each period (Baselga 2013). Two independent species distribution patterns, turnover (β_{SIM}) and nestedness (β_{NES}) were further assessed. The turnover pattern reflects the fish exchange and replacement among lakes, whereas if the fish composition in some lakes becomes a subset of lakes with greater fish richness, it shows a

nestedness pattern (Baselga 2010). The combination of these two opposing patterns together determines the regional dissimilarities. The mathematical relationship of the three indices can be simply expressed as $\beta_{SØR} = \beta_{SIM} + \beta_{SNE}$, and their respective computational equations are:

$$\beta_{SØR} = \frac{[\sum_{i<j} \min(b_{ij}, b_{ji})] + [\sum_{i<j} \max(b_{ij}, b_{ji})]}{2[\sum_i S_i - S_T] + [\sum_{i<j} \min(b_{ij}, b_{ji})] + [\sum_{i<j} \max(b_{ij}, b_{ji})]}$$

$$\beta_{SIM} = \frac{[\sum_{i<j} \min(b_{ij}, b_{ji})]}{[\sum_i S_i - S_T] + [\sum_{i<j} \min(b_{ij}, b_{ji})]}$$

$$\beta_{NES} = \frac{[\sum_{i<j} \max(b_{ij}, b_{ji})] - [\sum_{i<j} \min(b_{ij}, b_{ji})]}{2[\sum_i S_i - S_T] + [\sum_{i<j} \min(b_{ij}, b_{ji})] + [\sum_{i<j} \max(b_{ij}, b_{ji})]} \times \frac{\sum_i S_i - S_T}{[\sum_i S_i - S_T] + [\sum_{i<j} \min(b_{ij}, b_{ji})]}$$

where b_{ij} and b_{ji} are the fish species numbers exclusive to lake i and j, respectively, S_i is the richness of fish species in lake i, S_T is the regional fish richness, including all studied lakes (Baselga 2010). We calculated the multi-site dissimilarity, turnover, and nestedness patterns using the beta.multi function of the betapart (version 1.5.6) R package (Baselga et al. 2022).

Temporal pairwise fish dissimilarity between two periods

For each oxbow lake, we performed a pairwise comparison of species compositions between two periods to determine the degree of temporal change in fish assemblages. Similarly, this temporal species dissimilarity ($\beta_{sør}$) could also be extricated into species turnover (β_{sim}) and nestedness (β_{nes}) patterns between two periods (Baselga 2010). The three indices are formulated as follows:

$$\beta_{sør} = \frac{b + c}{2a + b + c}$$

$$\beta_{sim} = \frac{\min(b, c)}{a + \min(b, c)}$$

$$\beta_{nes} = \frac{\max(b, c) - \min(b, c)}{2a + \min(b, c) + \max(b, c)} \times \frac{a}{a + \min(b, c)}$$

where a is the number of shared fish species by both periods (the 2000s and the 2010s), b is the number of recorded fish species in the 2000s, and c is the number of fish only occurring in the 2010s. This pairwise dissimilarity calculations between two periods were calculated for each lake by utilizing the beta.pair function of the betapart (version 1.5.6) R package (Baselga et al. 2022).

Local and species contribution to dissimilarity

Legendre and de Cáceres (2013) proposed an approach allowing the calculation of the relative contributions of each fish species and oxbow lake to the regional dissimilarity based on a Hellinger-transformed fish incidence matrix. The Local Contribution to Beta Diversity (LCBD) and the Species Contribution to Beta Diversity (SCBD) can be calculated as $LCBD_i = SS_i/SS_{total}$ and $SCBD_k = SS_k/SS_{total}$, respectively. The SS_i and SS_k are the squared distances of lake *i* and species *k* to the dummy average community in a multivariate ordination distance space, respectively, and the SS_{total} is the sum of all SS_i or SS_k (Legendre 2014). An oxbow lake with a greater LCBD value denotes that the fish assemblage harbored there is relatively unique to other lakes, suggesting special local environmental conditions and conservation values (Vilmi et al. 2017; Wang et al. 2022). Meanwhile, a fish species with a larger SCBD value indicates that the distribution pattern of the species intensely influences the regional beta diversity (da Silva et al. 2018; Kuczynski et al. 2018; Xia et al. 2022). The LCBD and SCBD values were calculated for both the 2000s and the 2010s, respectively, using the beta.div function of the adespatial (version 0.3-20) R package (Dray et al. 2022).

Statistical analysis

We first assessed the respective temporal changes in average overall, native, and non-native fish richness across 28 oxbow lakes during two time periods. Next, we measured the multiple-site dissimilarity of fish assemblages and then decoupled it into turnover and nestedness based on the observed data in two periods, respectively. Further, following the same equations, we computed 100 simulated multiple-site dissimilarity indices by randomly sampling seven sites from the observed fish matrixes (Jiang et al. 2019). PERMANOVA tests with 9,999 permutations (Anderson 2001) were then utilized to test the statistical significance of the differences in the average values of the 100 simulated indices between the two periods, acting as the proxy of statistical significance of observed temporal changes in multi-site dissimilarity metrics. Subsequently, after estimating the degree of temporal changes in the fish composition of individual lakes over the decade (pairwise beta diversity), linear regressions between pairwise metrics of each lake and their distance from the river source (DRS) were performed to explore whether temporal changes in fish composition were associated with the longitudinal river gradient. Afterward, we estimated the temporal change of local and species contributions to regional dissimilarity ($\Delta LCBD = LCBD_{2010s} - LCBD_{2000s}$, $\Delta SCBD = SCBD_{2010s} - SCBD_{2000s}$). The oxbow lakes and fish species with significantly changed contribution values could be identified. Linear regressions were again applied to test whether the ΔLCBD of the oxbow lake also occurred in response to the longitudinal river gradient. Calculations for multi-site or pairwise dissimilarity indices, LCBD, and SCBD values were concurrently computed for overall, native, and non-native fish assemblages, respectively, in R (version 4.2.2) software (R Core Team 2022); PERMANOVA tests and linear regression analyses were performed in PAST (version 4.12) software (Hammer et al. 2001).

Results

Temporal change in fish richness

A total of 27 fish species were documented, of which 18 were classified as native and 9 as non-native (as presented in Table 1). There were 15 oxbow lakes with increased overall fish richness from the 2000s to the 2010s. Specifically for native and non-native fish assemblages, the proportion of non-native fish increased in 19 lakes, while native fish increased in only 3 of the 28 studied lakes. Regarding the regional average, overall fish richness and non-native richness increased significantly during the studied decade, with insignificant changes in native fish richness (Table 1).

Temporal change in regional dissimilarity and local/species contributions

While there was a minor increase in multi-site dissimilarity for the overall fish species, we found a significant decrease in species turnover and an increase in nestedness over ten-year periods. Nevertheless, inconsistent temporal trends were found when native and non-native fish species were examined separately. For the native fish species, dissimilarity and turnover increased significantly between the two periods. But for the non-native assemblages, both dissimilarity and turnover decreased, and only nestedness increased from the 2000s to the 2010s (Table 2, Fig. 2).

In terms of the overall fish community, the contribution of oxbow lakes to regional dissimilarity was relatively homogeneous in the 2000s (Fig. 3). However, the difference in local contribution to regional dissimilarity changed remarkably after a decade, with decreased contributions of upstream lakes and increased downstream contribution. Specifically for native fish faunas, relatively unique fish assemblages were found in the upper lakes in the 2000s. In contrast, the uniqueness of native fishes inhabiting these lakes declined remarkably in the 2010s. In general, the distribution patterns of

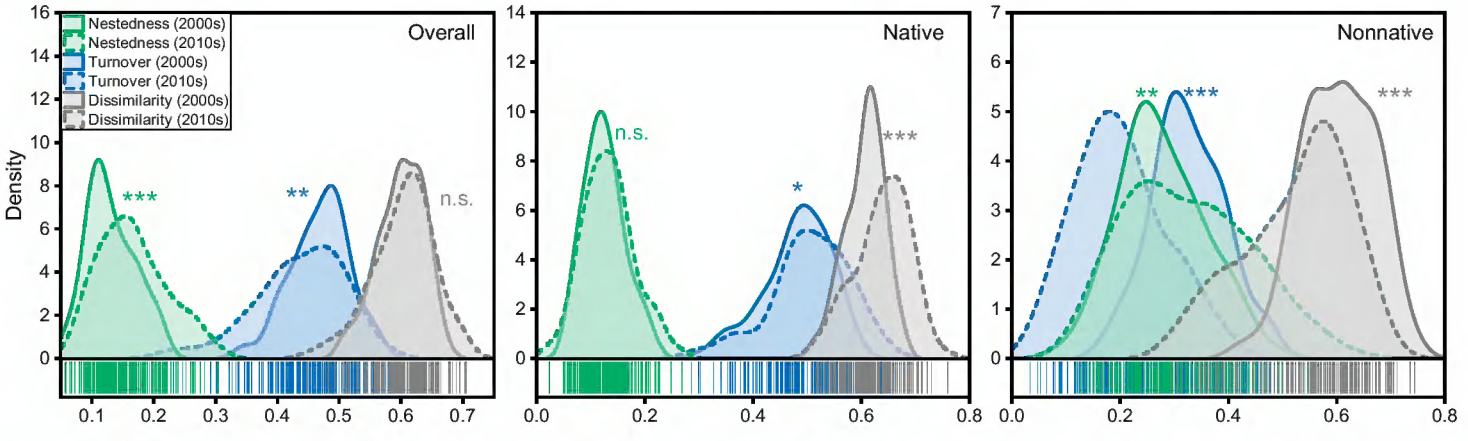

Figure 2. Distribution of simulated multiple-site dissimilarity metrics for overall, native, and non-native fish assemblages in the 2000s (solid lines) and the 2010s (dash lines). Overall dissimilarities (grey), as well as turnover (blue) and nestedness (green) components, were demonstrated in different colors. Frequency distributions were estimated by bootstrapping procedure (N = 100, with replacement) of seven sites per permutation to calculate multiple-site dissimilarities (denotes: ***: $p < 0.001$; **: $0.001 \leq p < 0.01$; *: $0.01 \leq p < 0.05$; n.s. = no significance: $p \geq 0.05$, based on PERMANOVA tests with 9,999 permutations).

Table 2. Regional multi-site dissimilarities of overall, native, and non-native fish faunas in the 2000s and 2010s, respectively. Multi-site turnover and nestedness patterns were also assessed. Based on dissimilarity metrics generated by multiple-site resampling simulations ($n = 7$, $N = 100$), statistical significance of differences in all dissimilarity metrics between two periods were tested by PERMANOVA (based on Euclidean distance index with 9,999 permutations). Differences that were statistically significant ($p < 0.05$) were marked as bold p values.

Metric	Overall			Native			Non-native		
	2000s	2010s	*p*	2000s	2010s	*p*	2000s	2010s	*p*
Dissimilarity	0.842	0.846	0.693	0.844	0.867	**0.001**	0.841	0.814	**0.001**
Turnover	0.763	0.741	**0.002**	0.766	0.791	**0.027**	0.636	0.487	**0.001**
Nestedness	0.079	0.105	**0.001**	0.078	0.076	0.215	0.205	0.327	**0.003**

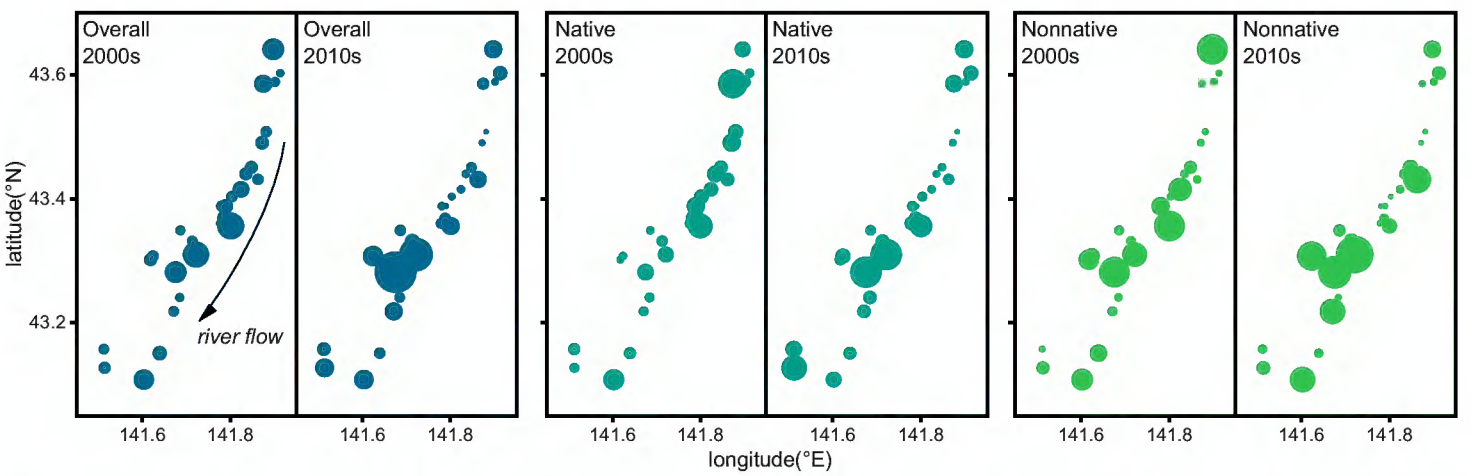

Figure 3. Local contributions to regional dissimilarity (LCBD) of overall (blue), native (green), and non-native (light green) fish faunas inhabiting each lake in the periods of the 2000s and 2010s, respectively. The dots represent the 28 oxbow lakes along the Ishikari River, and the dot size is proportional to the LCBD values of each lake.

LCBD for overall fish assemblages in the 2000s were similar to those of native fish faunas at that time, suggesting that the distribution of native fish dominated the community structure and spatial distribution of overall fish assemblages. Nevertheless, this dominance was surpassed by non-native fish in the 2010s, reflecting a spatial pattern of LCBD for overall fish assemblages that were similar to non-natives.

The characteristic distributional shifts of fish species were found during this decade based on ΔSCBD values for each species. Native fish species retained oxbow lakes in the upper reaches as habitats but lost occupancy in downstream oxbow lakes. However, non-native fishes showed two different patterns of distribution variations. One pattern was shrinking distribution to upstream lakes like native species; another occupied all oxbow lakes in the region (Fig. 4).

Regional patterns corresponding to dissimilarity changes

We found significant positive correlations between the distance from the river source and the temporal changes in species dissimilarity and turnover for both overall and native fish assemblages in each lake (Fig. 5). The findings indicate that oxbow lakes in the down-

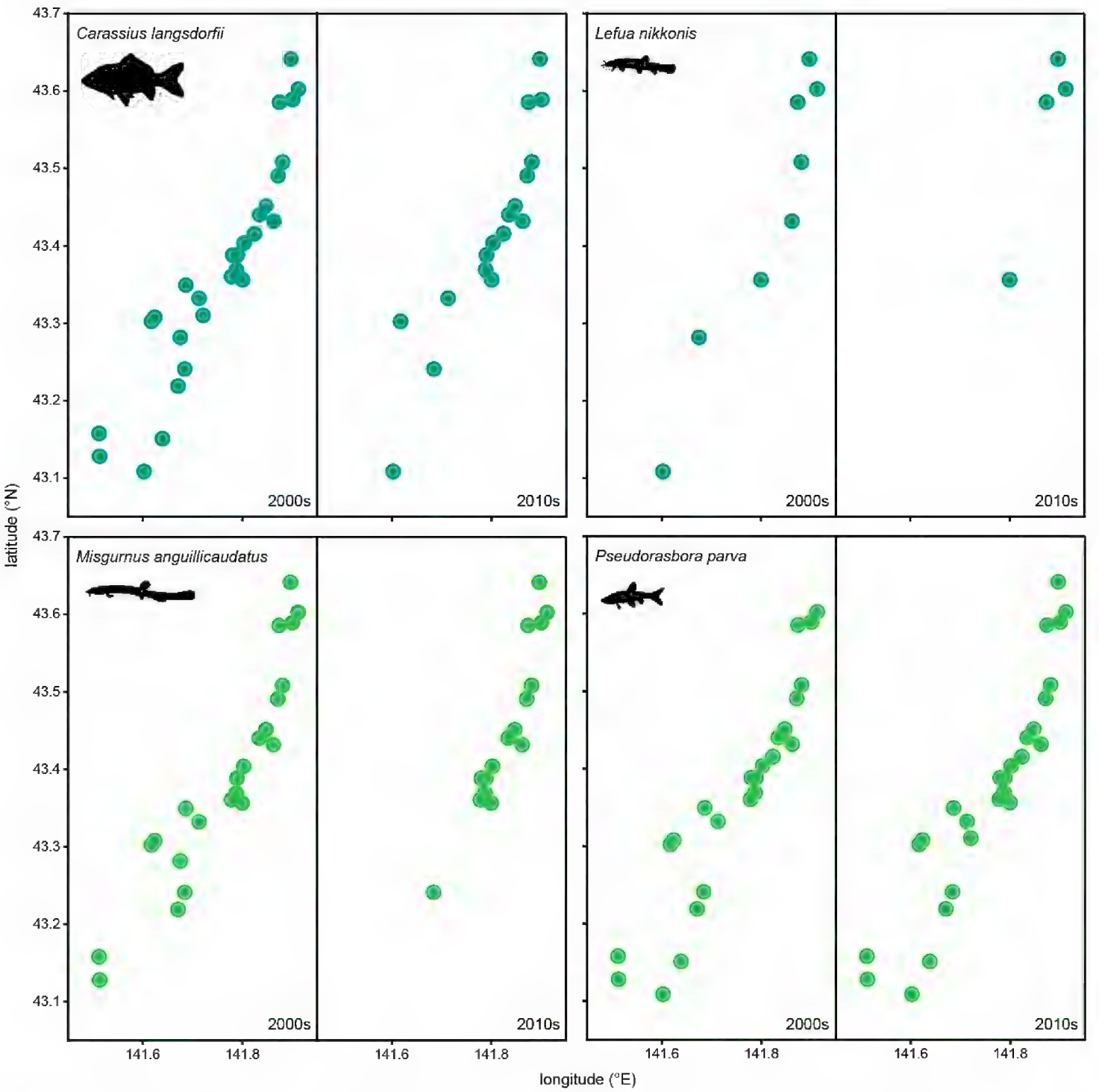

Figure 4. Map of distribution of the four most representative fish species in the 2000s and 2010s, respectively. The dots represent where the species has been recorded in the corresponding oxbow lakes. *Carassius langsdorfii*: native species with the most significant SCBD increase; *Lefua nikkonis*: native species with the most significant SCBD decrease; *Misgurnus anguillcaudatus*: non-native species with the most significant SCBD increase; *Pseudorasbora parva*: non-native species with the most significant SCBD decrease.

stream region have undergone more significant temporal shifts in species composition, particularly in native species turnover. However, the distribution of non-native species did not show a significant correlation with the spatial longitudinal gradient of the river.

There was a significant correlation between the temporal variation in LCBD values of oxbow lakes and their spatial location. While the LCBD values for overall and non-native fish assemblages were positively correlated with their lake location, the association was negative for native fish populations. Interestingly, regression analysis revealed that the location with the least temporal change in LCBD values is 110 km point afar from the source of the Ishikari River (Fig. 6).

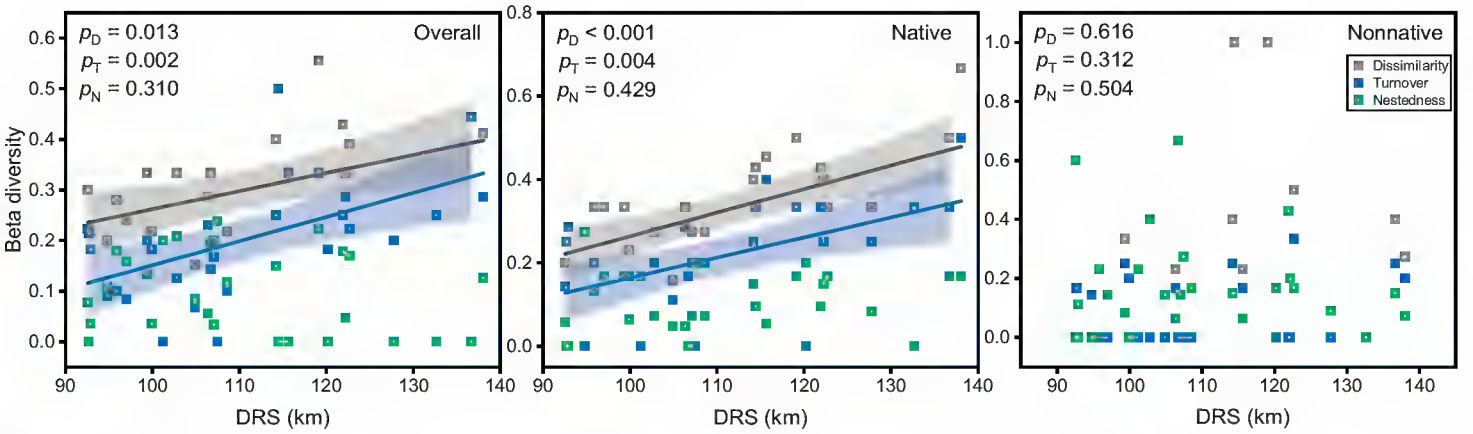

Figure 5. Linear regression relationships between temporal change in beta diversity (dissimilarity in grey, turnover in blue, and nestedness in green, y-axis) of overall, native, and non-native fish assemblages in each oxbow lake and their location, i.e., distances from the river sources (DRS, x-axis). The *p* value for each correlation pair is given. Only correlations with statistical significance ($p < 0.05$) are presented in solid lines.

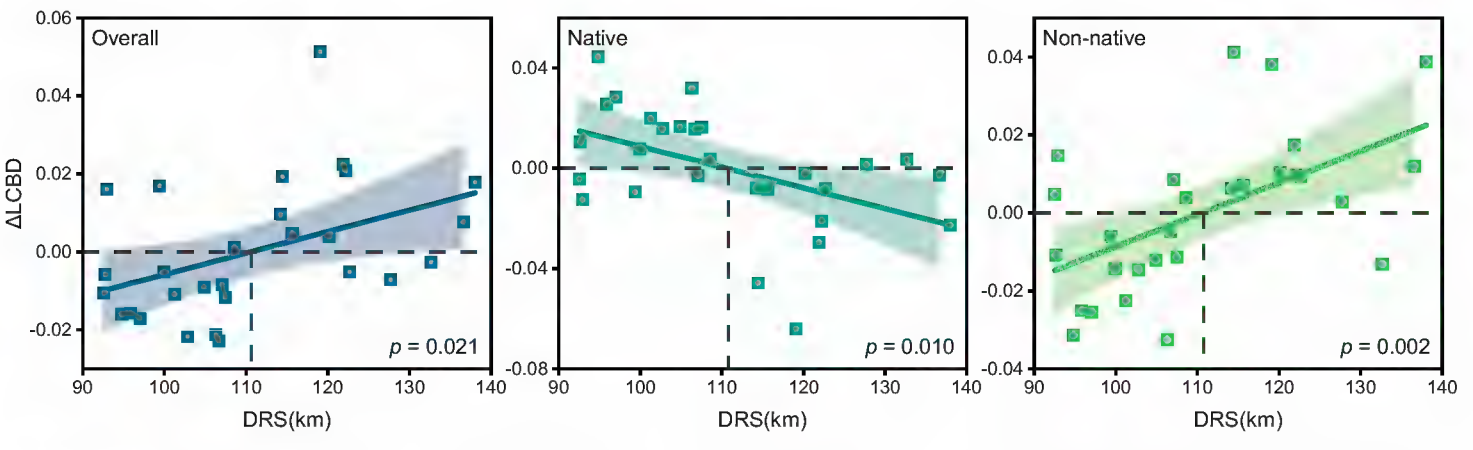

Figure 6. Linear regressions between the distance from the river source (DRS) and temporal change in LCBD values (ΔLCBD) of the 28 oxbow lakes for overall (blue), native (green), and non-native (light green) fish assemblages. The intersection of the fitted line with the horizontal dashed line indicates the theoretical location of the oxbow lake where there is no temporal change in the LCBD values (ΔLCBD = 0).

Discussion

Anthropogenic activities, including non-native fish introductions, have made freshwater fish homogenization an intractable issue around the world (Villéger et al. 2011; Su et al. 2021). This homogenization results in a reduction of the global species pool, a loss of phylogenetic diversity, and ultimately threatens ecosystem services and stability. Like many well-known hotspots for freshwater ecology research, such as the Great Lakes region in North America (Campbell and Mandrak 2019), the Yangtze River basin in Asia (Kang et al. 2018), and the Amazon region in South America (Arantes et al. 2018), etc., the far east high-latitude island represented by this study, is no exception to this trend. We found that introducing non-native fishes enriched the overall fish richness in oxbow lakes along the Ishikari River but significantly altered regional dissimilarity patterns: reduced turnover accompanied by higher nestedness. Such homogenization patterns were dominated by non-native species diversity patterns, demonstrating the most significant reduction in species turnover. The aggressive invasion of non-native species likely intensified interspecific competition and niche shifts in fish assemblages

(Lauzeral et al. 2011; Ishiyama et al. 2020; Liu et al. 2020) as a result of non-native invasions, native fish species were forced to occur sporadically in specific habitable oxbow lakes, leading to an increase in regional species turnover. The observed increase in native turnover reinforces the theory proposed by Socolar et al. (2016), which suggests that high community dissimilarity can serve as evidence of ongoing biodiversity degradation processes. In this scenario, a brief increase in community dissimilarity is followed by a dramatic decrease, culminating in a homogenous species composition in the region. Hence, it is essential to interpret the community dissimilarity results with caution.

We realized that the daunting change in the fish composition of the Ishikari River basin is tacit but rapid. Although the Ishikari River watershed is subject to a high population density and intense urbanization in Hokkaido, there were no apparent new major anthropogenic drivers or landscape alterations in the Ishikari River basins during the study periods (from 2003 to 2016). The differences in environmental conditions and land use between the upper and lower reaches were already in place before this study began (mainly formed in the last century). The relatively stagnant urbanization and land development during the study periods do not suggest that the non-native expansion was accelerated in line with the increased intensity of anthropogenic activities, as other studies reported (Anas and Mandrak 2021; Głowacki et al. 2021). In this context of little external environmental alteration, non-native fishes were still tacitly remodifying the fish community structures in the basin, suggesting the intense competitiveness of these non-native fish during inter-specific competitions with natives (Alves et al. 2017; Zhang et al. 2022). In addition, a recent study by Haubrock et al. (2021) reported shifts in fish communities over the last two centuries in the Arno River, Italy. Their results indicated an increase in non-native fish richness, with six newly established non-native species reported during the 1950s–2000s, a period marked by intensive industrial development. Afterward, a decrease of two non-native species was observed by 2015 (Haubrock et al. 2021), concurrent with a deceleration in anthropogenic modifications to the environment. When compared to the long-term time frame (decades, even hundreds of years) of the case study in Italy, the results from the present study in Ishikari watersheds in Japan demonstrate an expeditious expansion of non-native fishes over about only one decade, despite relatively little-changed environmental conditions during the study periods. While intermittent initiatives like fish stocking, fish ladder construction, and habitat restoration were in place in certain areas of the Ishikari watershed, our study advocates for exploring more comprehensive conservation strategies. The intent is to modify the status quo of native fish assemblages aiming toward the enhancement of their population size.

Identification of spatial distribution patterns of native fish is the cornerstone for establishing NFCAs to preserve endemism from invasions (Dauwalter et al. 2011; Williams et al. 2011). For many years, the within-site (alpha) diversity has been a cornerstone in developing conservation strategies and policies. For instance, regions with high alpha diversity are often accorded elevated conservation priority due to their likelihood of hosting a wide array of species, including endangered and endemic ones, thereby assuring enhanced levels of ecosystem services. However, recent studies have

begun to highlight the importance of incorporating between-site (beta) diversity into management decisions. Beta diversity, which takes into account not only the species richness but also the dissimilarities between different communities, provides a more comprehensive understanding of diversity loss processes (Baselga 2010). This information generated by dissimilarity analysis is crucial for accurately defining protected areas and ensuring their effectiveness in conserving biodiversity (Socolar et al. 2016; Dai et al. 2020; Jiang et al. 2020). The present study analyzed the temporal variation in fish assemblage dissimilarities along a longitudinal river gradient, revealing significant longitudinal differences. Specifically, more remarkable changes in fish species composition were observed in the downstream lakes, while upstream changes were relatively lower. These habitat occupancy patterns were reflected in the temporal variation of LCBD across the longitudinal lakes. A stark contrast was observed in the changes in native and non-native fish species, with the upstream lakes becoming increasingly crucial for native fish fauna and the downstream lakes for non-native fish assemblages. Remarkably, a point of equal change was identified at 110 km from the river source, where the upstream lakes still maintained a higher degree of uniqueness for native species, but non-native species dominated the downstream lakes. These results suggest that the displacement of native fish by non-native species progresses from downstream to upstream, with the dominance of non-native species extending up to 110 km from the river source after a decade. Based on these findings, it can be concluded that the conservation of native fish should be given priority in upstream lakes located less than 110 km from the source of the Ishikari River when establishing NFCAs (Walls 2018).

The variations in the external environmental conditions that these oxbow lakes, situated from up- to downstream watersheds, encounter offer a viewpoint to understand the fish community remodifications along the longitudinal gradient of the Ishikari River. The downstream oxbow lakes lie in Hokkaido's most extensive urban area (Duan et al. 2015). The impact of human activities, such as landscape alterations, hydrological and industrial facilities, agriculture activities, etc., could be considered triggers for the loss of native presences (Zhang et al. 2019; Boys et al. 2021; Pingram et al. 2021; Su et al. 2021). In the present context, it is noteworthy that certain non-native fish species, exemplified by the topmouth gudgeon (*Pseudorasbora parva*), exhibit robust adaptability and possess aggressive traits. Particularly, the topmouth gudgeon has displayed a remarkable capacity to tolerate and adapt to varying levels of Chemical Oxygen Demand (COD) in water, which serves as a widely accepted indicator of organic pollution resulting from domestic and industrial waste (Zhang et al. 2022). The high adaptability has facilitated their successful colonization, especially in lakes characterized by eutrophic conditions. Consequently, these non-native fish species have been able to complement and, in some cases, even outcompete native species within their ecological niches (Yamamoto et al. 2001; Zhang et al. 2022). Correspondingly, receiving minor disturbances from anthropogenic activities, the upper oxbow lakes provided heterogeneous shelters for fish assemblages, e.g., sufficient littoral shades and for sheltering, root mats and submerged woods for habitability, and less contaminated water quality for surviving, etc. (Lucas and Baras 2008; Garrett-Walker et al. 2020; Ishiyama et al. 2020; Pingram et al.

2021), thus maintaining relatively stable fish community compositions. Simultaneously, our results also demonstrated that the upstream lakes offered refuge for some non-native species that are less competitive in interspecific interactions. Nevertheless, it is imperative to remain vigilant to the potential that these non-native fish species, seeking refuge in the upstream oxbow lakes, may perpetuate the reduction of the ecological niche occupied by native fish species, presenting a continued danger to their survival.

The findings of this study confirm that there was a significant longitudinal gradient in the species composition alteration of native and non-native fish communities, with non-native species encroaching on native habitats from downstream to upstream oxbow lakes. On this basis, we propose utilizing the temporal change in the contribution of lakes to the regional dissimilarity (LCBD) as an indicator of potential protected areas for fish assemblages, which would reflect the competition between native and non-native fish species along the longitudinal river gradient. Despite the heterogeneous and fragmented administrative divisions within the basin typically making it challenging to the development of comprehensive conservation strategies that encompass the entire watersheds (Abell et al. 2007; Olden et al. 2010), this study provides a framework for determining the spatial range of these areas, which is the frontier point of the contest between the importance of native and non-native fishes. The proposed framework involves identifying waters that have increased in relative importance for native fish species as potential protected areas and then measuring along the longitudinal river gradient until waters that have not changed in importance are found. The position of these unchanged waters would then delimit the potential boundary of the protected region. Regular recalculation of the importance change can be used to monitor whether the position with no importance change has moved upstream or downstream. An upstream shift would suggest that the expansion of non-native fish species is ongoing. In contrast, a downstream shift would indicate the effectiveness of conservation and environmental efforts for native fish species. While we acknowledge the limitations of this framework in its simplicity and crudeness, we anticipate that through further validation and application in additional river basins, it has the potential to assist in identifying priority areas for the conservation of native fish species within the basin.

Conclusion

This study investigated the changes in the fish assemblage structures in 28 oxbow lakes in the Ishikari watershed in Japan spanning a decade. Results revealed a trend towards regional homogenization of fish assemblages, primarily driven by the rapid spread of non-native fish species, which resulted in an increase in nestedness patterns. Meanwhile, the sporadic occurrence of native fish species in specific lakes led to increased turnover patterns. Additionally, the changes in fish composition showed a significant association with longitudinal river gradients. The most significant changes were observed in downstream lakes close to urban areas, whereas the alterations in fish species in upstream lakes were relatively modest. The LCBD index assessments revealed that

downstream lakes were more susceptible to non-native invasions, leading to a homogeneous fish composition dominated by non-native species. This dominance was observed to be expanding upstream along the longitudinal river gradient, extending up to a point 110 km from the river source. In contrast, upstream lakes were found to be more natural and provided favorable habitats for native fish species. Our study, therefore, suggests that the NFCAs in the Ishikari River basin should be established in the oxbow lakes within the upper reaches range 110 km from the river source as a priority. Our findings provide an example of using alterations of species and local contribution to regional metacommunity dissimilarities to guide the delineation of conservation areas and can be applied in other riverine basins with significant longitudinal river gradients.

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Supplementary material 1

Fish incidence distributional data of oxbow lakes in the Ishikari River basin in the 2000s

Authors: Bingguo Dai, Junjiro N. Negishi, Kazuya Fujii, Md. Khorshed Alam, Zhongguan Jiang

Data type: Occurrences

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Supplementary material 2

Fish incidence distributional data of oxbow lakes in the Ishikari River basin in the 2010s

Authors: Bingguo Dai, Junjiro N. Negishi, Kazuya Fujii, Md. Khorshed Alam, Zhongguan Jiang

Data type: Occurrences

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Supplementary material 3

Geographical coordinates of the studied oxbow lakes in the Ishikari River basin

Authors: Bingguo Dai, Junjiro N. Negishi, Kazuya Fujii, Md. Khorshed Alam, Zhongguan Jiang

Data type: Coordinates

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